

Animal Communication: Origins of Sequential Structure in Birdsong

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Culturally transmitted behaviors have an innate foundation, but the detailed sequential structure of such complex, acquired behaviors is often an outcome of historical accidents. New research has identified innate predispositions for structuring vocal sequences in culturally acquired birdsong.

Stringing individual actions into complex sequences is a key feature of many culturally acquired behaviors [1,2].

Notable examples are spoken language and music in humans, and elaborate courtship displays, for example birdsong, in animals. But what determines the order of elements in a sequence, such as a musical piece, a spoken sentence or a song of a bird? Imagine an intelligent alien creature observing a person playing the piano. The alien will immediately discover that the sequential order of pressing the white and black piano keys is highly structured and repetitive. But this structure is, to a large extent, **idiosyncratic** to the piece being played. It is the weaker statistical regularities across different musical pieces that could potentially reveal to the alien what human music is about [3]. Such an investigation, however, must overcome two major obstacles. The first is of filtering out cultural biases that are specific to, for example, western music. The second obstacle is the need to filter out production biases stemming from motor constraints, such as the anatomy of our hands and relative positions of different keys on the piano. It is the residual sequential structure, once all these factors have been accounted for, that could eventually tell us something about the deep structure and function of music. As they report in this issue of *Current Biology*, James and Sakata [4] have managed to overcome the first obstacle of removing the **idiosyncratic cultural bias in birdsong** (where we play the role of the alien observer). They used a clever experimental design to control the

statistics of songbirds' acoustic environment during development, in a manner that allowed identification of innate predispositions for constructing song sequences.

Juvenile birds acquire their songs by imitating the songs of adults [5]. In this way, the vocal repertoire of one generation is culturally transmitted to the next, in a manner that often gives rise to local song dialects [6,7], a form of a stable polymorphic culture [8]. But the cultural transmission of song is not entirely open-ended. Song structure is learned within the boundaries of species-specific biases [9,10], which may be either strict or loose. At one extreme, the 'fee-bee' song sequence of the chickadee is similar across individuals, with a high pitch note invariably followed by a lower pitch note. At the other

extreme, Carolina thrashers produce highly irregular and complex song sequences. These sequences are not entirely random [11], but have little sequential regularity even within birds. James and Sakata [4] studied the zebra finch song, which is an intermediate case. On one hand, the zebra finch song is fairly simple, consisting of three to eight syllable types produced in a fixed order [12]. On the other hand, across individuals, there are no apparent trends in sequencing song syllables. Individual zebra finches can accurately imitate songs with an arbitrary arrangement of syllable types. For example, one can tutor a young zebra finch to produce a song composed of three syllables A–B–C, and then teach the same bird to transform its song into A–C–B, where all syllable

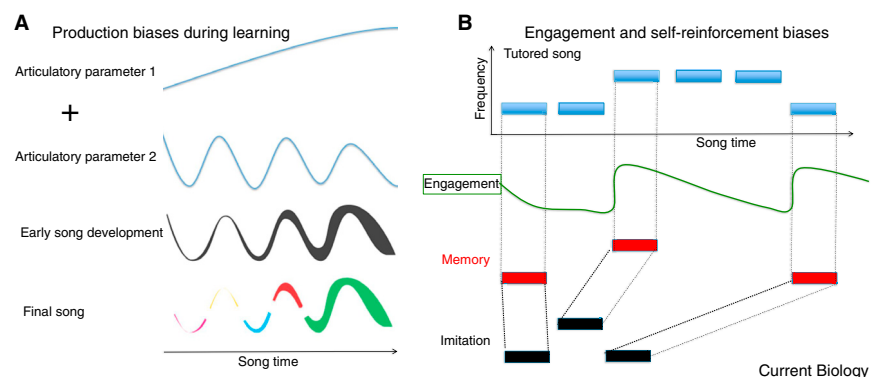


Figure 1. Putative mechanisms for song sequencing predispositions.

(A) A combination of two articulatory parameters, one oscillating and the other accumulating, may give rise to an oscillating gradient while the bird practices its song during early song development. Tutored songs with sequential structure of alternating frequencies and long final syllable may be learned more readily. Colored shapes represent emerging syllable types that match the tutored song. (B) While listening to a tutored song, a bird's attention might fluctuate between arousal and habituation. Such fluctuation in engagement might shape sequential biases in the imitation of the tutors' song.

transitions are reversed [13]. This combination of highly regular sequential order of song syllables within a bird, with no strict species-specific template for ordering syllables, allowed James and Sakata [4] to investigate 'soft' biases in the imitation of song sequences.

James and Sakata [4] presented young birds with a 'mix' of synthetic song playbacks, all composed of the same five syllable types, but in a random order, such that all possible syllable combinations were equally likely. Most birds learned the syllable types presented, but each bird developed a unique song with a particular, fixed syllable order. Comparing these songs across birds revealed two interesting deviations from the random (uniform) distribution of syllable order in the input songs. One trend was to alternate between low and high frequency syllables. The other was to place syllables of longer duration at the end of the song motif, and to place syllables of very short duration in the center of the motif. These trends could stem from production constraints, namely from birds' choosing the most 'convenient' syllable order in terms of articulation. A hypothetical scenario of song production peripheral dynamics [14] that may favor song sequences with oscillating syllable frequencies and longer syllables toward the end is presented in Figure 1A.

An even more interesting possibility is that the observed sequencing predispositions might mirror species-specific aesthetics. In this scenario, song acquisition may be driven by sensory or cognitive choices made by a young bird [15], either while listening to the songs of potential tutors, or while listening to itself during vocal practice. Consider birdsong as an ornament, or an 'object of desire' [15]. The level of arousal or pleasure that a young bird experiences as it listens to a tutor's song may bias (or even guide) the acquisition of syllable sequences. As illustrated in Figure 1B, sensory

habituation while hearing repetitions of similar syllables [16], and higher arousal while hearing transitions between syllables of different frequencies, could potentially bias song imitation towards the latter. Alternatively, 'self judgment' while the bird is practicing its early plastic song via auditory feedback could reinforce the imitation of more pleasing syllable transitions. In this way, a reinforcement-learning mechanism [17] could drive development of songs that provide higher self-pleasing song sequences, and by extension, making those songs more pleasing to a female bird listener during courtship.

The James and Sakata [4] study does not tell us if predispositions for sequential order in birdsong are driven by motor and perceptual constraints, or by aesthetic biases. But it opens the door for follow-up studies that would investigate the mechanistic foundation of these sequential propensities. We might be getting closer to identifying the innate factors that make birdsong so effective in influencing the behavioral state of bird listeners, perhaps in a similar manner that music affects human listeners [18].

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